

Two-Generation Analysis of Pollen Flow Across a Landscape. II. Relation Between Φ_{fi} , Pollen Dispersal and Interfemale Distance

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Manuscript received May 10, 2000

Accepted for publication November 10, 2000

ABSTRACT

We study the behavior of Φ_{fi} , a recently introduced estimator of instantaneous pollen flow, which is basically the intraclass correlation of inferred pollen cloud genetic frequencies among a sample of females drawn from a single population. Using standard theories of identity by descent and spatial processes, we show that Φ_{fi} depends on the average distance of pollen dispersal (δ) and on the average distance between sampled mothers (\bar{x}_i). Provided that mothers are sampled far enough apart ($\bar{x}_i > 5\delta$), Φ_{fi} becomes independent of \bar{x}_i and is then inversely proportional to the square of δ . Provided that this condition is fulfilled, δ is directly estimable from Φ_{fi} . Even when $\bar{x}_i < 5\delta$, estimation can easily be achieved via numerical evaluation. We show that the relation between Φ_{fi} and δ is only modestly affected by the shape of the distribution function, a result of importance, since this shape is generally unknown. We also study the impact of adult density within the population on Φ_{fi} , showing that to achieve the correct inference of δ from Φ_{fi} it must be taken into account, but that it has no effect on the distance at which mothers must be sampled.

MOST authors (*e.g.*, SLATKIN and BARTON 1989; NATH and GRIFFITHS 1996; BEERLI and FELSSENSTEIN 1999) have focused on the estimation of the “historical” migration rate, *i.e.*, the effective long-term average (HUDSON 1998). Such estimates are useful in understanding the evolutionary history of a set of populations, but they say nothing about the current level of gene flow, a more relevant predictor of contemporaneous (real-time) genetic exchange among a set of populations.

The need to estimate “real-time” gene flow rates has led to the design of direct estimators of gene flow. The most used method is currently paternity analysis (SCHNABEL and HAMRICK 1995), which is especially efficient when highly polymorphic markers are used (DOW and ASHLEY 1996; STREIFF *et al.* 1999), but conclusive analysis requires knowledge of the identity and genotypes of all potential males who could have contributed pollen to females within the stand.

Several studies (DOW and ASHLEY 1996; STREIFF *et al.* 1999) have now shown that a substantial portion of pollen comes from outside the stand, and it has become clear that characterizing all potential fathers that might have contributed pollen to the mothers within the stand is virtually a hopeless task. Lacking the ability to identify and/or evaluate the external males, paternity analysis can provide only a minimum estimate of average pollina-

tion distance across a landscape, sometimes a serious underestimate. Clearly, the estimation of real-time pollen dispersal must be addressed by some other means.

SMOUSE *et al.* (2001) have proposed a new estimation procedure, which uses only the genotypes of the mothers and of seedlings derived from them, along with the spatial positions of the mothers; the potentially contributing males are ignored. Using the sampled mothers as strata and their seedlings as replicates, one estimates the intraclass correlation of paternal gametes drawn from a single mother, Φ_{fi} , which is then used to estimate average pollination distance. Based on a simulation study, SMOUSE *et al.* (2001) have shown that Φ_{fi} is directly related to the decay parameter of the pollen dispersal curve.

The aim of this article is to address several questions that have been raised by that first study:

1. How is Φ_{fi} affected by the chosen dispersal function? It will be difficult to derive a valid estimate of the average pollen dispersion from an estimate of Φ_{fi} if that parameter is overly sensitive to the shape of the (usually unknown) distribution.
2. For any particular pollen dispersal distribution, what is the precise relation between Φ_{fi} and the dispersal rate?
3. How is the estimate of Φ_{fi} affected by the average physical distance from one sampled mother to another?
4. What is the impact of adult density within the reference population?

Answers to these questions should allow us to design a

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proper estimate of the average pollination distance from Φ_{it} . We develop the theoretical framework necessary to address these issues.

THE MODEL

General context: Assume that we have an infinite population, with adult individuals randomly distributed across the landscape, at density (d) per squared unit of distance. All individuals are monoecious and self-fertile, but they practice no more self-reproduction than would be expected at random. Allele frequencies are uniform across the landscape, all individuals are noninbred, and all have the same male fecundity. We assume that male gametes disperse independently and according to a probability distribution, to which we return below. We consider a sample of mothers drawn from among the adults, spaced an average distance of \bar{x}_i apart. Mothers are chosen on the basis of spatial locations, but not on the basis of their genotypes. We assume that spatial positions and genotypes of adults are not correlated.

The genetic diversity within and among the pollen clouds impinging upon the various mothers depends upon the pollen dispersal distribution. We focus here on two isotropic two-dimensional distributions of pollen dispersal: the normal distribution and the exponential distribution. In Cartesian coordinates measured from a single mother, assumed to be at coordinates (0, 0), the normal distribution with parameter σ will be

$$p(x, y) = \frac{1}{2\pi\sigma^2} e^{-(x^2+y^2)/2\sigma^2}, \quad (1)$$

where $p(x, y)$ is the probability (or more precisely the probability density function) that a single pollen grain will have been drawn from coordinates (x, y). We define a corresponding exponential distribution, with parameter γ , as

$$p(x, y) = \frac{1}{2\pi\gamma^2} e^{-\sqrt{x^2+y^2}/\gamma}. \quad (2)$$

Both have mean positions of (0, 0) in Cartesian coordinates, centered at the focal mother herself, and decline monotonically (and isotropically) in every direction. The average radial distance (δ) of pollen flow is calculated as the expected value of z , the average intermate distance:

$$\delta = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sqrt{x^2 + y^2} p(x, y) dx dy. \quad (3)$$

For the normal distribution, that yields

$$\delta = \sigma \sqrt{\frac{\pi}{2}}, \quad (4)$$

and, for the exponential distribution,

$$\delta = 2\gamma. \quad (5)$$

Figure 1 gives an example of the pollen distributions

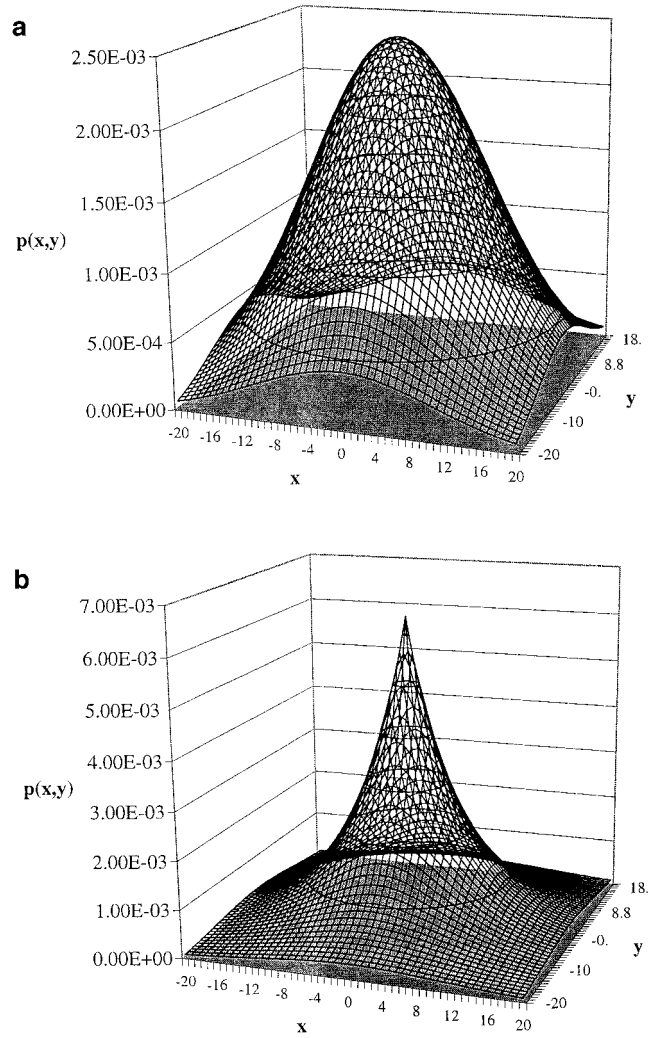


FIGURE 1.—Probability density function $p(x, y)$ plotted against the Cartesian coordinates (x, y), for the normal distribution (a) and the exponential distribution (b), for the same value of the average dispersal distance $\delta = 10$.

for both normal and exponential distributions, with the same average pollen dispersal distance, $\delta = 10$. These curves have very different shapes; the exponential distribution has a sharp peak at zero, but it also has a greater probability of reaching large dispersal distances.

The different shapes of the two distributions affect the dispersion of pollen distances for a given value of δ . One can gauge this dispersion via the variance of pollen dispersion, defined as $v^2 = E(z^2) - E^2(z)$, where $z = (x^2 + y^2)^{1/2}$ is the linear distance from the position of the pollinating male (x, y) to the index female (0, 0). Alternatively, one could use the mean squared distance $\eta^2 = E(z^2)$ from that same index female. In any case, all three measures (δ^2 , η^2 , v^2) are simple functions of the squares of the decay rate parameters of both the normal (σ^2) and exponential (γ^2) distributions. For the normal, the expected squared distance is

$$E(z^2) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} (x^2 + y^2) p(x, y) dx dy = 2\sigma^2, \quad (6)$$

from which we can compute η , the root-mean-square dispersal distance (LANDE and BARROWCLOUGH 1987),

$$\eta = \sqrt{E(z^2)} = \sigma\sqrt{2}. \quad (7)$$

We can extract the standard deviation, v , measured from the mean dispersal distance, δ , as

$$v = \sqrt{E(z^2) - E(z)^2} = \sigma\sqrt{2 - \pi/2}. \quad (8)$$

For the exponential, the corresponding root mean square and standard deviation are

$$\eta = \gamma\sqrt{6} \quad \text{and} \quad v = \gamma\sqrt{2}. \quad (9)$$

The probability that two seedlings, derived from the same mother, have the same father: The “genetic structure” of the pollen clouds of different maternal individuals is a function of the likelihood of drawing two pollen grains with alleles that are identical by descent. The first task is to compute the probability that two pollen grains from a single female are drawn from the same male, using the same reasoning as in WRIGHT (1946, 1969). The father of the first seed has coordinates (x, y) with probability $p(x, y)$. Since we assume a density of d across the landscape, the father of the second seed will be the same as the father of the first seed if his coordinates (x_2, y_2) fall in the square interval

$$\left[x - \frac{1}{2\sqrt{d}}, x + \frac{1}{2\sqrt{d}} \right], \left[y - \frac{1}{2\sqrt{d}}, y + \frac{1}{2\sqrt{d}} \right].$$

As shorthand, we denote that interval as $[x_-, x_+]$, $[y_-, y_+]$. The probability of that event is

$$\int_{x_-}^{x_+} \int_{y_-}^{y_+} p(x_2, y_2) dx_2 dy_2,$$

which is approximately $p(x, y)/d$, for d large enough. To a close approximation, we can write the probability (Q_0) that a female draws two different offspring from the same father as

$$Q_0 = \frac{1}{d} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p^2(x, y) dx dy, \quad (10)$$

which, for the normal distribution, becomes

$$Q_0 = \frac{1}{4\pi\sigma^2 d}. \quad (11)$$

We define the “effective pollen pool size” (N_{ep}) as $1/Q_0$ (SMOUSE *et al.* 2001). For the normal, that implies

$$N_{ep} = 4\pi\sigma^2 d. \quad (12)$$

This is the same as WRIGHT’s (1969, pp. 302–303) result for neighborhood size, defined as the inverse of the probability of identity by descent (IBD) for two uniting gametes. That is logical, since Wright was considering one male and one female gamete, dispersing with variance σ , whereas we are considering two male gametes, both dispersing with variance σ . Using (2) for the exponential distribution yields

$$Q_0 = \frac{1}{8\pi\gamma^2 d} \quad (13)$$

and thus an *effective pollen pool size* of

$$N_{ep} = 8\pi\gamma^2 d. \quad (14)$$

Note that for both distributions, Q_0 and N_{ep} are simple functions of σ^2 or γ^2 . Whether these results are converted into units of δ , η , or v , the essential information is to be found in the relevant decay rate parameter, σ or γ . The choice of parameterization is largely a matter of convenience, and for both normal and exponential cases, we find it useful to express Q_0 in terms of the average distance (δ) of pollen flow. For the normal distribution, by substituting (4) into (11), we obtain

$$Q_0 = \frac{1}{8\delta^2 d}, \quad (15)$$

and for the exponential distribution, by substituting (5) into (13), we obtain

$$Q_0 = \frac{1}{2\pi\delta^2 d}. \quad (16)$$

For equal average dispersal distances, $\delta^n = \delta^e$, the ratio of Q_0 values is (exponential:normal) = $8:2\pi \approx 1.273$, so for the same average pollen dispersal distance, the exponential yields a higher probability of a single female drawing two pollen grains from the same male, which amounts to a decrease in the effective size of her pollen pool.

The probability that two seedlings, derived from two different mothers, have the same father: Assume that these two females are at a distance x_1 apart. Without loss of generality, we set our system of Cartesian coordinates so that the first female is at position $(0, 0)$ and the second is at position $(x_1, 0)$. For a male at position (x, y) , the probability of fertilizing the first female is, as above, $p(x, y)$. For the same male, the probability of fertilizing the second female is $p(x - x_1, y)$. The probability $Q(x_1)$ that these two females are fertilized by the same male is

$$Q(x_1) = \frac{1}{d} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p(x, y) p(x - x_1, y) dx dy. \quad (17)$$

For the normal distribution, we obtain

$$Q(x_1) = \frac{e^{-x_1^2/4\sigma^2}}{4\pi\sigma^2 d} \quad (18)$$

(using Mathematica 4.0). For the exponential distribution, we have

$$Q(x_1) = \frac{1}{4\pi^2\gamma^4 d} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \exp\left(-\frac{\sqrt{x^2 + y^2} + \sqrt{(x - x_1)^2 + y^2}}{\gamma}\right) dx dy, \quad (19)$$

which can only be integrated numerically, for any given values of γ , x_1 , and d . Examples are given in Figure 2 for the normal and exponential distributions, for an

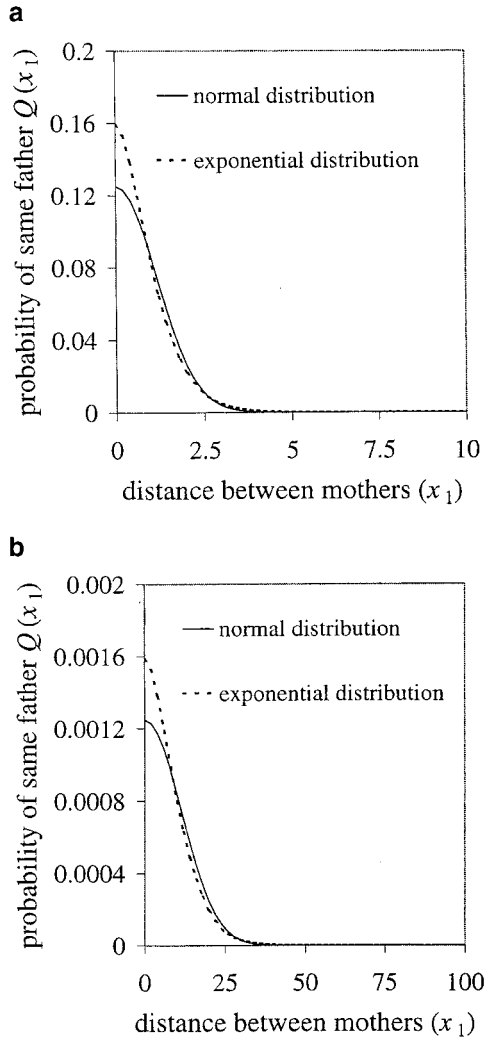


FIGURE 2.—The probability $\bar{Q}(x_1)$ that two genes, sampled from the pollen clouds of two mothers in the population, are derived from the same father, as a function of distance between the two mothers (x_1), for a density $d = 1$, obtained using (18) or (19). Results are given for the normal distribution and the exponential distribution, with average pollen dispersal distance $\delta = 1$ (a) or 10 (b). In all cases, this probability converges to 0 when the distance between mothers exceeds 5δ .

average pollen dispersal distance (δ) or 1 or 10. They show that $Q(x_1)$ falls to zero when the distance between mothers (x_1) is on the order of 5δ for either distribution, meaning that for $x_1 > 5\delta$, two mothers have almost no probability of being fertilized by the same father. This event is already rather unlikely for x_1 on the order of 3δ . The dependence of $Q(x_1)$ on average pollen dispersal distance is approximately the same for both distributions, the dependence attenuating over slightly greater distances when the exponential distribution is used.

Derivation of Φ_{it} : We define f_i , f_t , f_b , and f_p as the probabilities of IBD for different pairs of genes. For two alleles within an individual, $\text{pr}(\text{IBD}) = f_i$; for two pollen grains drawn at random from the pollen cloud of a single female, $\text{pr}(\text{IBD}) = f_t$; for two pollen grains drawn

at random from the pollen cloud of all females, $\text{pr}(\text{IBD}) = f_b$; and for two genes sampled at random from the whole population, $\text{pr}(\text{IBD}) = f_p$. For any of these quantities, $h_x = 1 - f_x$ will denote the diversity within that same compartment. We can relate Φ_{it} to these coefficients in the same way that F_{st} (NEI 1973; see also SLATKIN 1991) is related to the $\text{pr}(\text{IBD})$:

$$\Phi_{it} = \frac{f_t - f_i}{1 - f_t} = 1 - \frac{h_t}{h_i}. \quad (20)$$

To calculate h_t , the diversity within the pollen cloud of a single female, we must consider two genes sampled within this pollen cloud. These two genes come, with probability Q_0 , from the same father. In this case, they are derived from the same paternal chromosome with probability $1/2$ and cannot be different. Also, with probability $1/2$, they are derived from the different homologous chromosomes of the father and will then be different with probability h_i . Thus, two genes derived from the same father will, on average, be different with probability $h_i/2$.

On the other hand, these two genes will be drawn from different fathers, with probability $1 - Q_0$, in which case they will be different with probability h_p . Averaging over all cases,

$$h_t = \frac{Q_0}{2}h_i + (1 - Q_0)h_p. \quad (21)$$

To calculate h_b , the diversity within the pollen clouds of all sampled mothers, we must consider two genes sampled within the pollen clouds of different mothers. Mothers are, on average, at a distance \bar{x}_1 from each other. Provided that there is not too much variance of intermother distance, these two genes have approximately a probability $Q(\bar{x}_1)$, hereafter denoted \bar{Q} , of being drawn from the same father (see above). This yields, as in (21),

$$h_t = \frac{\bar{Q}}{2}h_i + (1 - \bar{Q})h_p. \quad (22)$$

We assume here no inbreeding among the adults themselves; *i.e.*, we set the inbreeding coefficient $F = 0$. This coefficient is defined as $F = 1 - h_i/h_p$, so for $F = 0$, we have $h_i = h_p$; *i.e.*, two genes sampled at random from within the same individual are neither more nor less likely to be identical than two genes sampled at random from the whole population, in which case, (21) and (22) become

$$h_t = \left(1 - \frac{Q_0}{2}\right)h_p \quad (23)$$

and

$$h_t = \left(1 - \frac{\bar{Q}}{2}\right)h_p, \quad (24)$$

respectively. Substituting (23) and (24) into (20) yields

$$\Phi_{ft} = \frac{Q_0 - \bar{Q}}{2 - \bar{Q}}. \quad (25)$$

For the normal distribution, and with no inbreeding, we obtain

$$\Phi_{ft} = \frac{1 - e^{-\bar{x}_1^2/4\sigma^2}}{8\pi\sigma^2d - e^{-\bar{x}_1^2/4\sigma^2}}. \quad (26)$$

For the exponential distribution, Q_0 can be calculated from (16), and $\bar{Q} = Q(\bar{x}_1)$ from the numerical integration given in (19), so we can calculate Φ_{ft} numerically.

If the sampled mothers are far enough apart ($\bar{x}_1 > 5\delta$), then $Q(\bar{x}_1)$ converges to zero (see Figure 2), and (26) simplifies to

$$\Phi_{ft} = \frac{Q_0}{2} = \frac{1}{2N_{cp}}, \quad (27)$$

or, translating into δ^2 , η^2 , and v^2 ,

$$\Phi_{ft}^n = \frac{1}{8\pi\sigma^2d} = \frac{1}{16\delta^2d} = \frac{1}{4\pi\eta^2d} = \frac{2 - \pi/2}{8\pi v^2d} \quad (28)$$

for the normal distribution, and

$$\Phi_{ft}^e = \frac{1}{16\pi\gamma^2d} = \frac{1}{4\pi\delta^2d} = \frac{3}{8\pi\eta^2d} = \frac{1}{8\pi v^2d} \quad (29)$$

for the exponential distribution. In both cases, Φ_{ft} is inversely proportional to the square of the dispersal parameter (γ or σ) and therefore inversely proportional to the square of (δ , η , and v); our preference is to use the average distance of dispersal (δ). As expected, Φ_{ft} increases with the distance between mothers (Figure 3), since the more distant the mothers are, the more differentiation is expected among their pollen clouds, all other parameters being equal. It follows that Φ_{ft} converges to the values given in (28) or (29), at the same rate as \bar{Q} converges to zero, reaching its asymptotic value when the average distance between mothers \bar{x}_1 is $\sim 5\delta$. Again, the approximation is reasonable even when \bar{x}_1 exceeds 3δ . For equal values of the mean dispersal distance ($\delta^n = \delta^e$), the ratio between the two Φ_{ft} values (at $\bar{x}_1 > 5\delta$) is

$$\frac{\Phi_{ft}^e}{\Phi_{ft}^n} = \frac{4}{\pi} \cong 1.273. \quad (30)$$

For equal values of the root mean squared error ($\eta^n = \eta^e$), on the other hand, we obtain

$$\frac{\Phi_{ft}^e}{\Phi_{ft}^n} = 1.500, \quad (31)$$

and if we equalize the standard deviations ($v^n = v^e$), we obtain

$$\frac{\Phi_{ft}^e}{\Phi_{ft}^n} = \frac{1}{2 - \pi/2} \cong 2.330. \quad (32)$$

For equal δ , the ratio is close to unity, and while the

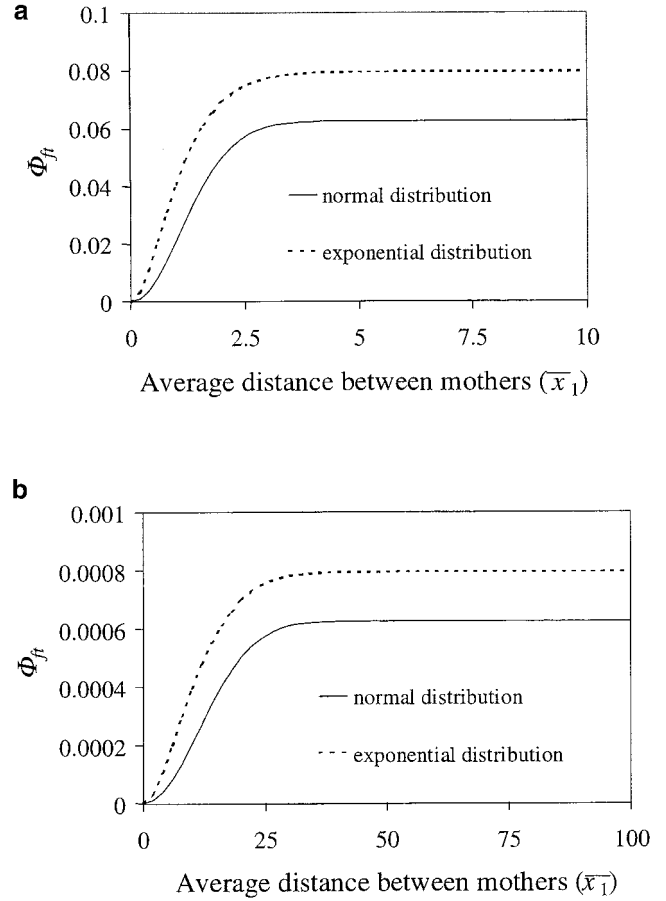


FIGURE 3.—Mothers' pollen cloud differentiation parameter (Φ_{ft}), obtained with (25), as a function of average distance between these mothers (\bar{x}_1), for a density $d = 1$. Results are given for the normal distribution and the exponential distribution with average pollen dispersal distance $\delta = 1$ (a) or 10 (b). In all cases, Φ_{ft} converges closely its value in (27) whenever the distance between mothers exceeds 5δ . The approximation is quite reasonable, even for $\bar{x}_1 > 3\delta$.

ratio is increased for equal η or equal v , Φ_{ft} is of the same order of magnitude, irrespective of the dispersal distribution. Increasing density (d) decreases Φ_{ft} for any given value of \bar{x}_1 , but the rates and patterns of Φ_{ft} convergence remain the same.

DISCUSSION

This study advances our understanding of the various parameters that might affect the estimation of pollen dispersal distance, using Φ_{ft} . One of the most important results is that the Φ_{ft} parameter will not depend upon distance between mothers (\bar{x}_1) and will be inversely proportional to the square of the average distance of pollen dispersal (δ), provided that mothers are sampled at a sufficient distance one from another (in practice, $\bar{x}_1 > 5\delta$). In that case, as estimate of δ can easily be extracted from an estimate of Φ_{ft} , which is available from an analy-

sis of the pollen pools of the various sampled females (SMOUSE *et al.* 2001).

This might sound useless from a practical point of view since in experimental situations δ is the unknown parameter to be estimated. If a rough estimate of this distance is already available, however, based either on previous genetic studies or on the observation of physical dispersal distance of pollen, mothers can be chosen so that all are at least five times more distant from each other than this rough estimate. If it later develops that mothers have been placed too close to one another, the estimate can be adjusted easily. An algorithm is described in the APPENDIX, for which both a C implementation and a DOS-executable file are available from F.A.

We also showed that the global diversity (h_p) of the marker loci employed has no effect on the relation between Φ_{it} and δ , and thus on the estimation of δ . It is noteworthy that the relation between F_{st} and Nm also does not depend on population-wide genetic diversity (WRIGHT 1951). Nevertheless, estimation variance for Φ_{it} increases when less polymorphic markers are used (SMOUSE *et al.* 2001), as expected, and it will therefore always be more useful to employ highly polymorphic markers when available, or to increase the number of markers employed, when minimally polymorphic markers are used.

An important result is that the basic form of the relation between Φ_{it} and δ is not affected by the choice of dispersal function, and while there are numeric consequences of the choice, they are not profound. This is of importance, since little is known about the shape of this dispersal function *a priori*, and to infer it (in detail) from genetic data would be prohibitively labor and cost intensive. The distance, beyond which two mother trees are unlikely to be fertilized by the same male, is only slightly larger for the exponential distribution than for the normal.

It is also interesting to note that, although increasing density (d) decreases Φ_{it} , it has no impact on the minimum distance at which mothers (\bar{x}_i) must be placed to ensure that Φ_{it} becomes independent of \bar{x}_i . This can facilitate experimental studies, since density can be ignored when the physical locations of mothers are selected.

We have assumed here that there is no undue degree of selfing, although an elevated/reduced selfing rate can be incorporated into the model. We have also ignored the possibility of past inbreeding for the adult generation, as well as the possibility that nearby males are more related to the female (and each other) than randomly placed males; but in real populations with restricted propagule flow, the probability of IBD among pollinating adults is expected to decrease with distance (MALÉCOT 1973). If there were "local structure" among the adults, even the pollen drawn from different males would yield increase in Q_0 and \bar{Q} , which would affect Φ_{it} . Variance in male fecundity and correlated dispersal

of male gametes (for example for vector-pollinated species) are also likely to occur in some cases, either of which would inflate our estimate of Φ_{it} . We leave these extensions for later communication.

We thank the other members of the TwoGener team, V. Sork, R. Westfall, and R. Dyer, as well as two anonymous reviewers, for helpful comments and suggestions on this manuscript. F.A. received a Formation Complémentaire par la Recherche grant from the French Ministère de l'Agriculture and a complementary grant from the North Atlantic Treaty Organization. P.E.S. is supported by McIntire-Stennis grant United States Department of Agriculture/NJAES-17309.

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Communicating editor: M. A. ASMUSSEN

APPENDIX: ALGORITHM FOR THE ESTIMATION OF THE AVERAGE DISTANCE OF POLLEN DISPERSAL FROM Φ_{it}

We assume here that an estimate of Φ_{it} is available from the study and that the average distance between mothers (\bar{x}_i) and the adult density (d) are known. Equation 27 allows estimation of an initial value of Q_0 from Φ_{it} : (i) From the initial estimated value of Q_0 , it is then possible to estimate a value of γ or σ , using (11) or (13),

(ii) using γ or σ , either Equation 18 or 19 then yields an estimate of \bar{Q} , (iii) given this estimated value of \bar{Q} , Equation 25 yields an updated estimate of Q_0 ,

$$Q_0 = 2\Phi_{it} + (1 - \Phi_{it})\bar{Q},$$

and (iv) which is used in (i) to compute a new value of γ or σ , and so on.

This recursive algorithm converges in no more than 100 iterations for the values we have tested and can be executed within a few minutes on an average PC computer. It yields estimated values for λ or σ that can be directly transformed into an estimate of the average distance of pollen dispersal (δ), using (4) or (5), or into η and v , using (7)–(9).